Chemical element dynamics in decomposing leaf litter

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Received February 23, 1978

LOUSIER, J. D., and D. PARKINSON. 1978. Chemical element dynamics in decomposing leaf litter. Can. J. Bot. **56**: 2795–2812.

Chemical element change in decomposing aspen and balsam poplar leaves was followed for 60 months in an aspen woodland site in southwestern Alberta, Canada. The changes in concentration and weights of the various elements and in several C:element and element:element ratios are discussed and compared with literature findings and with the concentrations, weights, and ratios encountered in the soil layers.

The initial concentrations of all elements, except K and Na, were similar in both aspen and balsam leaf litter; K was higher initially in balsam leaf litter and Na was higher initially in aspen leaf litter. In the decomposing leaf litter, the concentrations of N, Ca, Zn, Mg, Fe, Mn, Cu, and Na generally increased with time while the concentrations of P and K decreased. A decrease in weight was noted for N, P, K, Ca, Mg, and Zn during decomposition while an increase was found for Fe, Mn, Cu, and Na. The order of mobility of elements after 60 months in decomposing aspen and balsam leaf litter was K > Na > P > Zn > Mg > Ca > N > Mn > Cu > Fe. The effects of site aspect on elemental loss, the elemental change in aerial litter bags, the components of elemental change, and models of elemental loss are discussed.

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Les auteurs ont suivi, pendant 60 mois, les changements dans la composition en éléments chimiques au cours de la décomposition de feuilles du *Populus tremuloides* et du *P. balsamifera*, dans une tremblaie du sud-ouest de l'Alberta au Canada. Ils discutent les changements de concentration et de poids des divers éléments et de différents rapports carbone:élément et élément:élément. Ils comparent les valeurs obtenues à celles rapportées dans la littérature ainsi qu'aux poids et aux rapports qui existent dans les horizons du sol.

Les concentrations initiales de tous les éléments, excepté le K et la Na, étaient semblables chez le *P. tremuloides* et le *P. balsamifera*: le K était plus élevé au départ dans la litière du *P. balsamifera* alors que dans la litière du *P. tremuloides* c'était le Na qui était le plus abondant. Dans les litières en décomposition les concentration de N, Ca, Zn, Mg, Fe, Mn, Cu et Na ont augmenté en général avec le temps alors que les concentrations de P et K ont diminué. Il y a eu diminution en poids de N, P, K, Ca, Mg et Zn au cours de la décomposition alors que des augmentations se sont manifestées pour le Fe, Mn, Cu et Na. Après 60 mois, la mobilité des éléments dans les litières du *P. tremuloides* et du *P. balsamifera* était K > Na > P > Zn > Mg > Ca > N > Mn > Cu > Fe. Les auteurs discutent les effets de la station sur la perte en éléments, les changements en éléments dans des sacs de litière aériens, les composantes du changement en éléments, et des modèles de perte d'éléments.

[Traduit par le journal]

Introduction

Nutrient elements retained in particular plant parts, e.g., leaves, twigs, bark, and reproductive materials, at the time of physiological death are returned to the soil surface as plant litter. The subsequent release of these elements during decomposition completes, and begins again, the cycling of elements within the soil–plant system. The rates at which these nutrients are utilized in unaltered terrestrial ecosystems are determined mainly by the rates at which those elements are released from plant litter by decomposition (Thomas 1970). Particular patterns of litter fall, humification, and decomposition are characteristic for differing forest types, and these are the factors determining the course and rate of the recycling of nutrients (Olson 1963).

This paper describes chemical element release from decomposing *Populus tremuloides* Michx. and *P. balsamifera* L. leaf litter in the litter decomposition experiments reported in Lousier and Parkinson (1976). The dynamics of element release were followed over 60 months and were compared with the spatial and temporal dynamics of soil elements described in a paper by Lousier and Parkinson.[1] Some C:element and element:element ratios have been determined to help in distinguishing release patterns. The C:element ratios indicate the relationships of element release patterns to dry weight losses: i.e., if the ratio increases, the element is being released through leaching or mineralization processes; if the ratio decreases, the element is being accumulated either biologically or physicochemically; and if the ratio remains constant, the release of the element is related to dry weight loss. The numerical value of the C:element ratios is termed critical if it is the value at which the element begins to be released or if it represents the heterotroph demand for the element. Element:element ratios can indicate loss pattern relationships (and possible biological and (or) chemical relationships) between elements: i.e., is a particular element limiting and do limiting elements as well as any other elements influence the recycling of other elements?

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[1] Lousier, J. D., and D. Parkinson. Organic matter and chemical element dynamics in an aspen woodland soil. In preparation.

The objectives of this paper are (1) to follow the changes in concentration and weight of N, P, K, Ca, Mg, Mn, Fe, Na, Cu, and Zn in decomposing leaf litter; (2) to describe the effects of site aspect on chemical element change in decomposing leaf litter; (3) to determine chemical element change in aerial litter bags; (4) to assess the components of elemental change; and (5) to discuss elemental loss models.

Site Description

The main study site was a cool temperate aspen woodland at 1400 m in the front range of the Rocky Mountains, Alberta, Canada (51°2′ N, 115°4′ W). The woodland was on a well-drained, south-facing slope at the northern end of the Kananaskis Valley. The climate of the region is essentially continental, characterized by short, dry summers and relatively long cold winters with intermittent, warm, chinook winds (Kirby 1973). The soil has been classified in the orthic gray luvisol subgroup (Karkanis 1972) and has a surface organic horizon that is easily divided into L, F, and H layers (Lousier 1974). Data on some soil and atmospheric conditions for the region were given in Lousier and Parkinson (1976).

The tree layer of vegetation was dominated by trembling aspen (*Populus tremuloides* Michx.), with balsam poplar (*P. balsamifera* L.) being less frequent in occurrence. The understory was composed mainly of various grasses and herbs and of wild rose shrubs. More details on the vegetation of the area were given in Dennis (1970) and Lousier (1974).

Five other aspen stands with north and (or) northwest exposures were selected as auxiliary plots (Lousier and Parkinson 1976). These plots were completely deciduous and were as similar as possible to the main aspen woodland plot in terms of tree density, type, age, and species of understory vegetation.

Methods

Leaf Litter Decomposition

Two sets of tree leaf litter decomposition experiments were carried out: a long-term study, covering 5 years and using 10-mm mesh hairnets as litter bags, and a short-term study, lasting 3 years and using 3-mm mesh square litter bags (Lousier and Parkinson 1976). For both of these two groups of experiments, leaves of aspen and balsam were caught in aboveground nets, air dried to a constant weight for 3 weeks (at 21°C), enclosed in litter bags, and placed in field plots. The long-term study bags were sampled annually while the short-term study bags were sampled at the following intervals after placement in the field: 1, 5, 8, 12, 18, 24, 30, and 36 months. At each sampling time, the retrieved bags were returned to the laboratory, extraneous material was removed, and the wet weight of the leaf material was measured. The material was reweighed after oven-drying at 80°C for 48 h. The contents of each bag were then analyzed chemically.

Chemical Analysis

The dried samples of each litter type were lumped and mill ground, and a subsample was analyzed on a CHN analyzer (Hewlett-Packard, model 185) for the total carbon, hydrogen, and nitrogen. Separate subsamples were acid digested (nitric acid – perchloric acid) and were analyzed for Ca, Mg, K, Na, Zn, Mn, Cu, and Fe by atomic absorption spectrophotometry (Perkin-Elmer, model 303), and for total phosphorus by the molybdenum blue method.

Results and Discussion

Elemental Change

The changes in concentration and amount of each element over the 60-month experimental period in aspen and balsam litter are illustrated in Fig. 1. Sample size for each point plotted was one because all the bags of each litter type at each sampling time were combined and mixed; the samples for chemical analysis were taken from this composite. Consequently, the data presented in Fig. 1 are without confidence limits. Changes in some C:element and element:element ratios are listed in Table 1.

Those elements that increased in concentration with the depth of the litter bag in the litter layers (in other words, the age of the leaf litter) were N, Ca, Zn, Mg, Fe, Mn, Cu, and Na. Those that increased with depth in the soil layers were Fe, Mn, Na, Cu, Zn, and K. The concentrations of P and K decreased with age of litter while the concentrations of Ca, Mg, P, and N decreased with depth in the soil layers. All the elements studied increased in abundance with depth in the soil layers, while Fe, Mn, Cu, and Na increased and P, K, Ca, Mg, N, and Zn generally decreased in weight with the age of the litter. The initial concentrations of all elements except K and Na were similar in both aspen and balsam leaf litter; Na was higher initially in aspen and K was higher initially in balsam leaf litter. Based on the information in Fig. 1, the order of mobility of elements after 60 months in decompos-

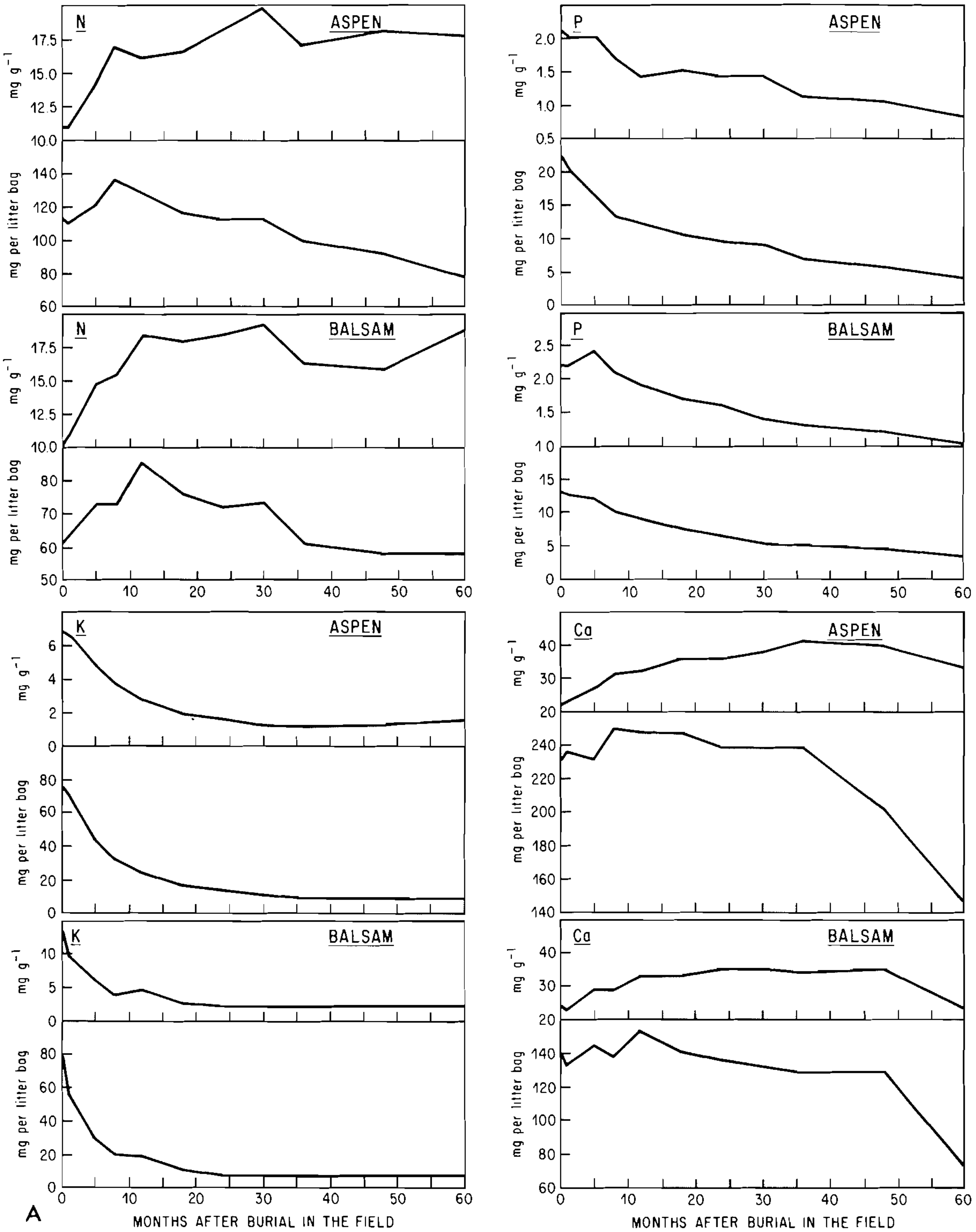

FIG. 1A. Changes in concentration and weight of N, K, P, and Ca over the first 60 months of decomposition of leaf litter on the soil surface.

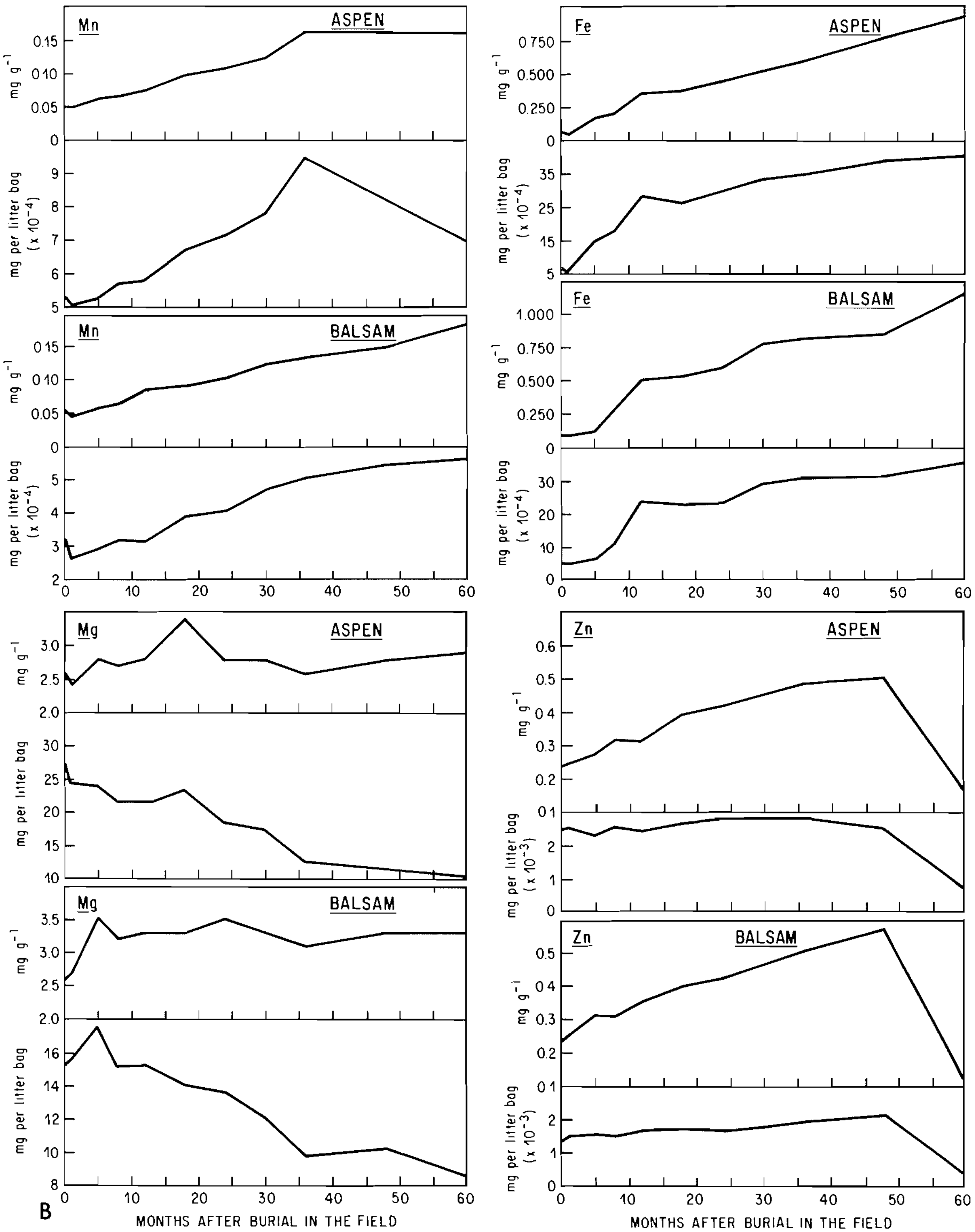

FIG. 1B. Changes in concentration and weight of Mn, Mg, Fe, and Zn over the first 60 months of decomposition of leaf litter on the soil surface.

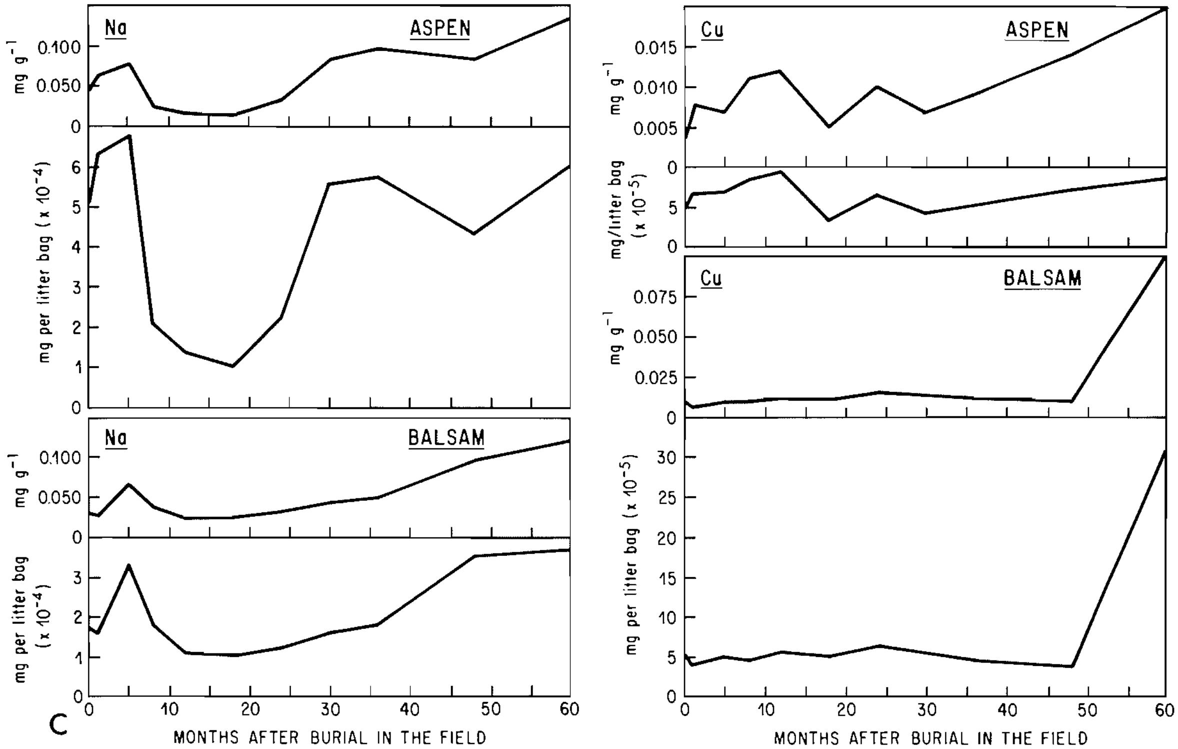

FIG. 1C. Changes in concentration and weight of Na and Cu over the first 60 months of decomposition of leaf litter on the soil surface.

ing aspen and balsam leaf litter was K > Na > P > Zn > Mg > Ca > N > Mn > Cu > Fe, comparing generally with mobility series from a few limited studies reported in the literature (Kornev 1959; Remezov 1961; Marchenko and Karlov 1963; Rochow 1975; Rapp 1971; Wood 1974; Krauter 1976) and differing from others (Attiwill 1968; Boyd 1971; Lemée and Bichaut 1973; Ulrich *et al.* 1971; Cole *et al.* 1967; Reiners and Reiners 1970; van Cleve and Noonan 1975; Töth *et al.* 1975; Gosz *et al.* 1976) (Table 2).

The results of this study are comparable with and complementary to those compiled by Hodkinson (1975) for terrestrial plant litter decomposing in a beaver pond ecosystem about 1.5 km east of the aspen woodland and by Krauter (1976) for decomposing *Epilobium angustifolium* L. leaves and stems in the aspen woodland study site. Further data on chemical input by various litter components are available in Cragg *et al.* (1977).

Nitrogen

N in forest litter is in short supply and most of it is therefore retained, primarily by the microorganisms (Gosz *et al.* 1973). During decomposition the amount of carbon is progressively reduced, thus causing an increase in N concentration. This does not, however, explain increases in weight of N in the litter bags. Various authors have attempted to explain such increases in weight of N: microbial fixation of atmospheric N (Olsen 1932; Remacle 1970, 1971; Lemée and Bichaut 1973; Wood 1974), throughfall (Gilbert and Bocock 1960; Bocock 1963, 1964), dust, insect frass, and green litter (Bocock 1963), and fungal immobilization and (or) translocation (Harley 1971; Anderson 1973*b*; Gosz *et al.* 1973; Wood 1974); depending on localized environmental conditions, any or all of the above phenomena may act in some combination to increase the amount of N in the litter in the aspen woodland. The increase in weight of N in the aspen and balsam leaf litter occurred during the first 8 to 12 months of decomposition, i.e., before being covered by subsequent tree leaf litter fall, and during the period of maximum weight loss and leaching. Chemical analyses of aerial aspen litter bags (Table 5) indicated a substantial increase in N concentration over the course of 10 months to levels similar to those in aspen litter bags on the ground. Dry weight loss and fungal biomass in these aerial bags was substantially and statistically significantly less than in the ground-surface litter bags (Visser,

TABLE 1. Changes in the C:element and some element:element ratios in decomposing aspen and balsam leaf litter

Tree	Time, months	C:N	C:K	C:P	N:P	K:P	C:Ca	N:Ca	Ca:P	C:Mn	C:Mg	Mg:P	C:Fe	Mn:Fe	C:Zn	C:Na	C:Cu
Aspen	0	45.48	69	234	5.2	3.4	23	0.50	10.5	9 824	189	1.1	7797	0.79	2108	10 024	98 240
	1	44.94	69	243	5.5	3.5	21	0.48	11.5	9 906	202	1.3	7957	0.80	1989	7 829	60 675
	5	35.13	96	245	7.0	2.6	18	0.52	13.5	8 062	176	1.4	2810	0.35	1835	6 225	70 257
	8	29.72	157	296	10.0	2.4	16	0.55	18.2	7 612	186	1.6	2284	0.30	1605	19 323	45 673
	12	30.43	123	352	11.4	1.6	15	0.50	22.9	6 572	176	2.0	1343	0.20	1574	27 383	41 075
	18	30.35	154	334	11.3	1.6	14	0.47	24.0	5 109	147	2.3	1303	0.26	1294	33 380	100 140
	24	26.75	232	348	12.1	1.5	14	0.47	25.7	4 507	174	2.0	1077	0.24	1167	14 318	48 680
	30	24.85	289	351	12.9	1.2	13	0.47	27.1	3 968	176	2.0	925	0.23	1098	5 857	70 286
	36	26.70	287	418	15.5	1.5	11	0.41	37.3	2 801	209	2.0	763	0.27	955	4 639	51 033
	48	25.01	252	454	18.0	1.8	11	0.45	40.0	2 788	198	2.3	588	0.21	911	5 284	32 457
	60	26.80	240	599	22.5	2.5	14	0.53	42.5	2 939	200	3.0	511	0.17	2818	3 422	23 955
Balsam	0	47.78	39	233	4.6	6.0	21	0.41	10.9	9 494	197	1.2	5634	0.59	2172	17 679	56 967
	1	46.61	52	233	5.0	4.5	22	0.48	10.5	11 146	190	1.2	5634	0.51	2010	18 310	73 243
	5	35.32	87	216	6.3	2.5	18	0.52	12.1	8 800	148	1.5	4056	0.46	1686	7 749	51 920
	8	33.46	132	245	7.1	1.9	18	0.52	13.8	7 691	161	1.5	2270	0.30	1666	13 213	51 530
	12	28.42	113	273	9.5	2.4	16	0.55	17.4	6 037	157	1.7	1026	0.17	1467	21 633	43 267
	18	26.92	193	283	10.6	1.5	15	0.55	19.4	5 295	146	1.9	904	0.17	1208	19 272	40 150
	24	25.80	226	297	11.9	1.3	14	0.54	21.9	4 564	136	2.2	790	0.17	1122	15 313	29 669
	30	23.55	215	323	12.9	1.5	13	0.51	25.0	3 646	161	2.0	585	0.16	976	10 764	32 293
	36	27.44	214	345	12.3	1.6	13	0.47	26.2	3 347	172	2.0	549	0.16	895	9 153	37 375
	48	29.22	211	388	13.3	1.8	13	0.46	29.2	3 121	166	2.3	543	0.17	822	4 795	46 510
	60	25.36	207	476	19.0	2.3	21	0.83	23.0	2 602	170	2.8	414	0.16	4178	3 936	4 811

personal communication) which indicated that accumulation of N may have occurred and that a major portion of this accumulation of N may have been caused by nonbiological phenomena, perhaps some of those mentioned above. This situation may also hold for N dynamics in litter bags on the litter surface as well.

Very little N is released as nitrate until the C:N ratio of the organic matter has been lowered through decomposition; consequently those plant materials with high C:N ratios decompose at a slower rate than those with a lower C:N ratio. Fluctuations in C:N ratios are due primarily to variations in the N supply (Tisdale and Nelson 1966): when N is deficient, carbohydrates will be deposited in vegetative cells, causing them to thicken and resulting in a higher C:N; when N supplies are adequate, proteins are formed from the manufactured carbohydrates, resulting in less deposited carbohydrate, more protoplasm, and a lower C:N. N has been reported to decline gradually in amount in leaves from the time of leaf maturation to leaf senescence (Curlin 1970), and Cragg *et al.* (1977) found a drop of 70% in N concentration in aspen leaves during the growing season.

Lutz and Chandler (1946) reported critical C:N ratios for forest soils ranging generally from 20:1 to 30:1; at ratios greater than this N was immobilized; at ratios less than this, N was mineralized. The beginning of a decrease in weight of N in aspen after 8 months and in balsam after 12 months suggested that a process of net mineralization was occurring. The C:N ratios at 8 months for aspen and 12 months for balsam were below 30:1 for the first time during decomposition and had reached the average annual C:N ratio for the L layer (Table 3). The weight of N per litter bag dropped below the initial weight (at 0 months) only after 30 months of decomposition in aspen and 36 months in balsam.

Potassium

K appears to be completely water soluble in plants but may combine with some organic compounds, e.g., be adsorptively bound to proteins (Olsen 1948). K is concentrated in the young leaves, buds, and root tips but declines gradually and substantially in amount from aspen leaf maturation to leaf senescence (Tew 1970; Cragg *et al.* 1977). The principal primary sources of K in forest soils are insoluble parent minerals (which, under the influence of CO_2 and water, produce a small quantity of exchangeable, plant-available K) and easily decomposable inorganic and organic compounds.

Lousier and Parkinson (1976) considered dry weight loss in decomposing aspen and balsam litter and described two major components of this litter

TABLE 2. Comparison of mobility series of elements being released from different types of decomposing leaf litter in different habitats throughout the world

Location	Vegetation	Element mobility series*	Reference
Canada	*Epilobium angustifolium*	K > P > Mg > Ca > N	Krauter 1976
	Populus tremuloides *P. balsamifera*	K > Na > P > Zn > Mg > Ca > N > Mn > Cu > Fe	This study
Australia	*Eucalyptus obliqua*	Na > K > Ca > Mg > P	Attiwill 1968
	E. delegatensis	K > P > Mg > N > Ca	Wood 1974
U.S.S.R.	Russian hardwoods	K ≥ P > Mg ≥ Ca	Kornev 1959; Remezov 1961; Marchenko and Karlov 1963
Hungary	*Quercus petraea*	K > Mg > Na > Zn > Mn > Ca > Fe > N > P	Töth *et al.* 1975
	Q. cerris	K > Mg > Na > Zn > N > Mn > Fe > Ca > P	Töth *et al.* 1975
	Cornus mal	K > Mg > Na > Zn > Ca > P > N > Fe > Mn	Töth *et al.* 1975
	Acer campestre	Mg > K > Na > Mn > Fe > Zn > Na > Ca > P	Töth *et al.* 1975
Germany	*Fagus* forest	Mn > K > Ca > P > N > Mg > Fe	Ulrich *et al.* 1971
Belgium	*Quercus* forest	K > P > Mg > N > Ca	Rapp 1971
	Carpinus forest	K > P > Ca = N > Mg	Lemée and Bichaut 1973
	Fagus forest	K > Mg > Ca > P > N	Lemée and Bichaut 1973
	Quercus forest	K > Mg > P > Ca > N	Lemée and Bichaut 1973
U.S.A.	*Pseudotsuga menziesii*	K > Ca > N > P	Cole *et al.* 1967
	Juncus effusus	Na ≥ K > Mg > N > P > Ca	Boyd 1971
	Quercus forest	Ca > Mg > P > N	Reiners and Reiners 1970
	Quercus forest	K > Mg ≥ P > Ca ≥ N	Rochow 1975
	Populus tremuloides (50 year old)	K > Ca > Mg > Zn ≥ P > N > Mn > Fe	van Cleve and Noonan 1975
	P. tremuloides (120 year old)	K > Ca > Mg ≥ P > Zn > N > Mn > Fe	van Cleve and Noonan 1975
	Betula papyrifera (50 year old)	K = Zn > Mn ≥ Mg ≥ P > Ca > N > Fe	van Cleve and Noonan 1975
	B. papyrifera (120 year old)	K > Mg ≥ Zn ≥ P ≥ Ca > Mn > N > Fe	van Cleve and Noonan 1975
	Northern hardwoods	K > Mg > Ca > Mn > Zn > N ≥ P > Ca > Na > Fe	Gosz *et al.* 1976
	Potamogeton diversifolius	K > Na > Mn > Zn > Mg > Fe > Ca	Wohler *et al.* 1975

*Based on rates of loss from decomposing litter or on turnover rates.

TABLE 3. Average annual C:element and element:element ratios in the soil layers (to a depth of ~8 cm)

Soil layer	C:N	C:K	C:P	N:P	K:P	C:Ca	N:Ca	Ca:P	C:Mn	C:Mg	Mg:P	C:Fe	Mn:Fe	C:Zn	C:Na	C:Cu
L	27.2	209	385	13.8	2.1	16	0.6	23.7	5315	232	1.6	463	0.08	1578	11 540	48 017
F	19.2	242	328	16.6	1.4	14	0.7	23.1	3239	212	1.5	327	0.10	1045	10 695	34 086
H	17.8	115	314	17.5	2.8	14	0.8	21.6	1446	377	1.1	99	0.07	8785	370	29 900
Ah	11.7	18	204	16.9	11.7	43	2.4	7.1	248	166	1.4	7	0.03	380	63	4 022
Ae	7.5	5	82	10.4	17.2	28	3.2	3.3	129	51	1.8	1	0.01	241	19	1 261

based on the rate of decomposition: a fast decomposing component and a slow decomposing component. The fast decomposing component appeared to have disappeared within the first 12–18 months of decomposition. It was during this time span that 70–80% of the K in aspen and 80–90% of the K in balsam litter were lost. These results were consistent with those of Kucera (1959), King and Heath (1967), Attiwill (1968), Gosz *et al.* (1973), Wood (1974), and Töth *et al.* (1975) in various other field decomposition studies. Despite the rapid initial loss of K, there was some correlation with dry weight loss, $r = 0.9399$ ($p = 0.05$) for aspen litter and $r = 0.9040$ ($p = 0.05$) for balsam litter.

The similar, minimum final concentrations of K in aspen and balsam litter, with the twofold difference in initial concentrations, may have represented a quantity of K that may have been immobilized by heterotrophs and that may have indeed comprised the heterotroph demand for K (Gosz *et al.* 1973). The slow increase in K concentration after attainment of minimal levels noted by Gosz *et al.* (1973) and the slight increase at 60 months noted in the present study may have indicated the beginnings of larger increases in K concentrations with the depth of the litter in the soil profile. The minimum levels of K concentration in decomposing aspen and balsam leaf litter were found to be less than those in the L layer but very similar to those in the F layer (Lousier and Parkinson, see footnote 1). The concentrations of K in the H layer were almost twice as high as those in the F layer and indicated some mechanism of K accumulation in the aspen woodland soil. Stark (1972), Todd *et al.* (1973), Ausmus and Witkamp (1974), and Cromack *et al.* (1975) have shown that fungal hyphae, rhizomorphs, sporocarps, slime molds, and actinomycetes concentrated K very readily and could thus serve as significant K sinks in the soil system. Hinneri (1975) stated also that the bulk of the mineral content in macrofungi consists of K.

C:K ratios followed increase–decrease patterns similar to those in the soil layers (Table 3), i.e., increases from L to F layers, decreases from F to H to Ah layers, explained primarily by the decrease–increase in K concentrations. Because the minimum levels of K reached in aspen (after 36 months) and balsam (after 24 months) litter may be considered the heterotroph demand, the critical C:K ratios are 290:1 for aspen and 225:1 for balsam litter.

Phosphorus

P is a constituent of many compounds in plants and, along with N and K, is classed as a major nutrient element. However, in most plants, it occurs in smaller quantities than do N and K. An adequate supply of P early in the life of a plant is necessary for the primordial development of its reproductive parts. The production of seed is regulated by the content of stored phosphorus in the plant, and seeds are endowed with high concentrations of P, ensuring normal nutrition of seedlings in their initial stages of development (Wilde 1958). P has a high mobility in plant tissues, being translocated, according to the plant's needs, from the leaves to the growing regions.

Attiwill (1968) concluded that the loss of P was associated with the loss of dry matter throughout decomposition, while Gosz *et al.* (1973) and Töth *et al.* (1975) found that the concentration and amount of P increased over time. In the present study, there was good correlation between dry weight loss and P loss ($r = 0.9951$ for aspen litter, 0.9819 for balsam litter, $p < 0.05$) suggesting that net mineralization occurred from the time of burial of the litter bags in the field. In the initial states of decomposition, P was lost faster from aspen; i.e., after 12 months, 46% of the P in the aspen litter had been released while only 32% of the P in the balsam litter had been lost. This rate of loss suggested a high susceptibility of P to leaching processes, even though Ryden *et al.* (1973) showed that P was not readily leached through soils.

Attiwill (1968) emphasized the importance of the redistribution of P within the tree before autumn leaf fall in the Australian hardwoods and contrasted this with Russian hardwood data (Kornev 1959; Remezov 1959), which showed little or no movement of P from leaves prior to litter fall. Tew (1970) showed a decrease in P concentration over the growing season but found no change in percentage dry weight of P from mid-July to leaf senescence for aspen leaves in Utah, and his figure for P concentration at leaf senescence was similar to those for aspen and balsam at leaf abscission in this study. Concentrations of P in aspen leaves at the time of leaf abscission from groves in the southern Alberta aspen parkland (Dormaar 1971) were found to be similar to those recorded by Tew (1970) and in this study. Cragg *et al.* (1977) also found a decrease in P concentrations in aspen leaves over the summer in the aspen woodland. However, Dormaar (1971) showed that P concentration in balsam leaves substantially exceeded those recorded in this study. Hence, there appeared to be minimal redistribution of P in aspen leaves because of approaching leaf senescence but possibly a high amount of P translocation in balsam leaves. Nevertheless, both aspen and balsam leaf litter in this study may have had relatively more P to be leached after leaf fall.

The pattern of P loss did not appear to be consistent with what might have been predicted from the results of the organic layer analyses given in Lousier and Parkinson (see footnote 1), i.e., the concentration of P increased from the L layer to the F, and the weight of P increased from L to the F to the H layers. It was possible that several sources of P input (e.g., plant reproductive materials, green litter fall) may have been excluded by the 3-mm mesh size of the litter bags.

The C:P ratios of the decomposing litter equalled those in the L layer only after 30–36 months' decomposition of aspen litter and 36–48 months for balsam litter. Whereas the C:P ratios of the soil layers decreased with depth (Table 3), those in decomposing litter increased, even after the L layer levels had been achieved. Because P is such an essential element for biological activity and because mineralization appeared to begin at the time of litter fall, the critical C:P value is about 230:1 for both aspen and balsam leaf litter.

P is often limiting to vegetative growth and thus must be recycled quickly. The recycling of P may thus have an effect on or reflect the recycling of other elements; if this is so, it will be reflected in P:element ratios (Gosz *et al.* 1973). The N:P ratios increased throughout the course of the study and reached L layer levels after the same time intervals as C:P ratios. L layer N:P ratios were slightly less than those in F, H, and Ah layers. The N:P results disagreed somewhat with those of Gosz *et al.* (1973, 1976) who found a correlation between the N and P in decaying litter, indicated by similar N:P ratios in the decomposing litter, litter fall, the soil layers, net stemflow, and throughfall. These authors also found a highly significant positive correlation between N and P concentrations for litter from all the species of tree studied. The present study indicated a negative correlation ($0.10 > p > 0.05$) between N and P concentrations in decomposing litter. P may be extremely limiting in the Kananaskis site, and, hence, be in high demand, and may be recycled very quickly either within the soil and litter organism biomass or within regular nutrient pathways, or both. Barsdate *et al.* (1974) concluded that the cycling of P was not directly linked to the cycling of carbon, and grazed microbial systems cycled P faster than nongrazed systems.

K:P ratios in the decomposing litter first decreased (as in the transition from L to F layers) and then increased (as in the progression from F to H layers). P appeared to be more closely related to dry weight loss than did the more rapidly released K.

Calcium

Calcium is not a major nutrient element but is required by all higher plants. A large portion of the Ca found in many trees is located in the leaves and, in some species, is precipitated in the cells as salts, e.g., carbonate and oxalate. Ca is necessary for plant growth and imparts rigidity to the cell wall (Uhrstrom 1969) and is also found as a structural constituent of the middle lamella (Tisdale and Nelson 1966). The amount of Ca increases in the leaves throughout the growing season and is retained until major structural breakdown of the leaves occurs (Burges 1956; Tew 1970). Cragg *et al.* (1977) found a 127% increase in Ca concentration in aspen leaves over the course of the growing season.

There may be a direct relationship in soils between Ca and ion uptake in general (Tisdale and Nelson 1966; Jorgensen and Wells 1973), and Ca in the soil tends to overcome the injurious effects of higher levels of Na, K, Mg, Al, and Mn (Wilde 1958). Although most of the forest soil Ca exists in fairly insoluble inorganic forms, substantial amounts (up to 40%) exist in exchangeable form in the colloidal complex. As a result of the relatively high amounts of Ca in their litter, many hardwoods favour accumulation of this element in the surface soil to a greater extent than do most conifers (Alway *et al.* 1933). Ca held in exchangeable form is highly mobile and is readily replaced by H^+, and, consequently, can be readily leached from the surface organic layers (Lutz and Chandler 1946; McLean 1975). A high content of Ca in the litter increases the amount of exchangeable Ca in the soil, reduces soil acidity, favours the development of mull humus layers, and stimulates the activity of the soil flora and fauna (Lutz and Chandler 1946; Jorgensen and Wells 1973). Ca was the most abundant cation measured in the aspen soil and in the decomposing litter. This was understandable because the bulk of the mountain material in the area is limestone, which predominates in the parent material of the soils of the region (Kirby 1973).

Will (1967), Attiwill (1968), Thomas (1960, 1970), and Gosz *et al.* (1973) indicated that Ca was less susceptible to leaching than K or Mg and that decomposition was responsible for most of the Ca loss, i.e., the loss pattern of Ca was similar to dry weight loss patterns of the leaf tissue. Tóth *et al.* (1975) found accumulation of Ca or very slow release of Ca with time in oak forest leaf litter, and the present study indicated similar Ca loss dynamics: loss patterns unlike those for the dry weight loss (i.e., C:Ca ratios decreasing for the first 48 months of decomposition) and a poor correlation (r = 0.56–0.60, p = 0.05) between Ca weight loss and dry weight loss. Ca was concentrated for 48 months in both types of leaf litter but to a greater degree in aspen litter. Consequently, the weight of Ca in the litter bags dropped below the initial levels sooner in balsam (after 18 months) than in aspen (after 36 months). The concentrations attained in the aspen litter were in some cases 30% greater than those in the L, F, and H soil layers, whereas the concentrations of Ca in the balsam litter were similar at the various stages of decomposition to those in the L, F, and H layers (Lousier and Parkinson, see footnote 1).

Wood (1974) attributed an increase in Ca concentration in leaf litter in some cases to differential removal by leaf-feeding invertebrates of tissues of relatively low Ca concentration but this could not explain the present increases in weights of Ca. The aspen site lacked such leaf-feeding organisms (Mitchell 1974; Carter 1975) so one must consider such external sources of Ca as dust, precipitation, and weathering of parent material as important sources of Ca in an area with a preponderance of limestone material. Several studies have shown that considerable amounts of Ca can be added to the soil by precipitation and foliar leaching (Attiwill 1966; Carlisle *et al.* 1966, 1967; Duvigneaud and Denaeyer-de Smet 1967, 1970; Ovington 1968), and Thomas (1969) noted that most of Ca leached from the canopy was retained in the litter layer and not leached through to the mineral soil. Stark (1972), Todd *et al.* (1973), and Cromack *et al.* (1975) noted the role of some fungal structures in concentrating Ca; Stark (1972) indicated that such accumulated elements were not susceptible to leaching from live or dead intact structures and Cromack *et al.* (1975) provided an hypothesis accounting for ecosystem cycling of Ca in basidiomycetes.

The C:Ca ratios in the L, F, and H layers were similar (Table 3) and the ratios in the decomposing leaf litter reached these levels after 8–12 months. The increase in the C:Ca ratios at 60 months was consistent with the pattern in the soil which showed increases from the H to the Ah layers. The critical C:Ca levels were not apparent because of the abundance of Ca. N:Ca ratios fluctuated little over the 60-month period, except that at 60 months for balsam, the N:Ca ratios almost doubled to the level found in the H layer. This seemed to indicate a N–Ca relationship similar to the N–P relationship described by Gosz *et al.* (1973); however, it appears that no biological conclusions can be drawn from what may simply be a coincidental N–Ca relationship. Ca:P ratios might have been expected to be fairly stable because of the literature correlations of both elements with dry weight loss, but because of the continual release of P an increase was observed. Ca:P levels in decomposing litter reached those of the soil L, F, and H layers (L ≡ F ≡ H) after 12 months in aspen and 24 months in balsam.

Manganese

Cragg *et al.* (1977) found the Mn increased in concentration in aspen leaves over the growing period. Töth *et al.* (1975) showed an increase in concentration of Mn but generally a slight decrease in weight of Mn during decomposition. Gosz *et al.* (1973) found that the concentrations and amounts of Mn generally decreased during decomposition. The results in this study contradicted those data and suggested very similar patterns of accumulation for Mn and Fe. These elements are somewhat similar in function in plant tissues (e.g., enzyme activation) and many of the conditions influencing the availability of the reduced forms of Mn and Fe are similar (Alexander 1967). The rate of accumulation of Mn was probably governed by many of the same variables as was the rate for Fe, and the exogenous sources of Mn appeared to be similar.

The concentration of Mn in the soil layers increased 50% from L to F, doubled from the F to the H layers, and doubled from the H to the Ah layers (Lousier and Parkinson, see footnote 1), so an increase in Mn concentration with time in decomposing litter was expected. Mn appeared to be accumulating faster in the litter bags than in the L or F layers in the soil, reaching L and F layer concentrations in 18 and 36 months respectively. The C:Mn ratios in the litter reached the L layer levels at 18 months and the F layer levels at 30–36 months. Accumulation of Mn was positively but nonsignificantly ($p > 0.10$) correlated with dry weight loss in aspen litter and positively and significantly ($p = 0.05$) correlated with dry weight loss in balsam litter. Stark (1972) found only slight accumulation of Mn in fungal material, namely rhizomorphs and slime molds. Byrne *et al.* (1976) reported that Mn was not accumulated by macrofungi, and Mn requirements of fungi have been concluded to differ from those of vascular plants (Cochrane 1958).

Magnesium

The Mg concentrations recorded in decomposing aspen and balsam litter, although fairly stable for most of the 60 months, were consistently and substantially higher than those in the soil layers and the final concentrations were higher than the initial concentrations of Mg. The only period when Mg increased in concentration or weight was over the winter suggesting higher Mg contents in snow. However, these increases were usually followed by immediate, and sometimes equal, decreases, probably due to leaching. Wood (1974) found higher Mg concentrations in litter in small mesh bags, so these litter bags perhaps cause Mg to be concentrated in the litter within.

Attiwill (1968) found Mg loss similar in pattern to Ca loss, viz., more or less similar to the rate of dry weight loss. Gosz *et al.* (1973) and Töth *et al.* (1975) suggested that the Mg loss pattern was much like that of K: a very rapid loss (up to 80%) in the first 6 months of decomposition. Wood (1974) reported that variations in concentration of Mg were not correlated with rate of decomposition, or with rainfall, temperature, soil organic carbon, and soil pH. The results of the present study indicated that Mg loss was more similar to P loss. Despite its relative leachability (Attiwill 1968; Tukey 1970), Mg was not as leachable as K and was therefore not released as rapidly. Mg loss was correlated positively but not strongly ($r = 0.8937$ for aspen, 0.8845 for balsam, $p = 0.05$) with dry weight loss. After 12 months, 20% of the original Mg in aspen had been released but none of the Mg in balsam had been lost. After 24 months, the percentages were aspen 30%, balsam 10%; after 60 months, aspen 60%, balsam 45%.

Tew (1970) found that Mg concentrations in aspen leaves increased over the growing season while Cragg *et al.* (1977) showed a 20% decrease in Mg concentration from June to late August and a 70% increase from late August to late September. Attiwill (1968) maintained that 36% of the Mg in leaves was withdrawn before leaf fall and Ca was immobilized in plant parts prior to litter fall. Because much of the leaf Mg in plants is organically as well as inorganically bound (De Kock 1958), there may have been a Mg immobilization in aspen and balsam leaves before litter fall. This could account for the Mg loss patterns shown in Fig. 1, i.e., less leachable Mg and slower decomposition release of Mg. Mg does not seem to be accumulated as readily by fungi as some of the other elements, although Mg has been found to accumulate in rhizomorphs (Stark 1972) and basidiomycete mycelia (Burges 1956), and fungi have high Mg requirements for metabolism and growth (Cochrane 1958). Consequently, there may be less of a heterotroph demand for Mg than other elements in the aspen soil system.

The C:Mg ratios in the decomposing litter did not reach the levels recorded in the soil layers (Table 3) because of the elevated Mg concentration in the litter. However, the levels in the L and F layers were similar and the C:Mg ratios followed this pattern generally throughout the study period. The minimum concentrations of Mg indicated that the critical C:Mg ratio was 209:1 for aspen and 170:1 for balsam litter. Mg and P have some important physiological corelationships in plants (Miller 1957; Wallace and Mueller 1962) and should perhaps retain some of this corelation in the litter and soil. Mg:P ratios in the soil layers were reasonably constant with depth but increased up to threefold in decomposing litter to levels about twice those in the soils, indicating a faster release of P than Mg. All these discrepancies were due to the higher Mg concentrations in the litter; no explanation was obvious as to why they were higher.

Iron

The amount of Fe in forest soils depends on the nature of the parent material and the climatic conditions under which the soils developed. Fe occurs in forest soils as primary minerals and as anhydrous and hydrous oxides in the colloidal complex. Fe is relatively immobile and the amount of Fe present in exchangeable form depends on soil pH and on conditions of oxidation and reduction. It is probable that most forest soils have sufficient supplies of available Fe for most of the deep-rooted vegetation (Lutz and Chandler 1946).

It has been found that Fe increased in concentration in growing aspen leaves (Cragg *et al.* 1977). Fe accumulation in soil and litter layers is dependent primarily on microbial activity (Gosz *et al.* 1973). The rate of Fe accumulation in decomposing leaf litter will vary greatly with source, form, microbiological activity, pH, and other environmental conditions (Gosz *et al.* 1973). There are various sources of Fe that could have produced the accumulation patterns in the aspen and balsam litter: foliar leaching, dust, green litter fall, weathering of parent material, upward percolation during the very wet periods in the soil, and interactions with low molecular weight organic acids and humic and fulvic acids.

The patterns of increase in concentration and amount of Fe were expected because Fe increased in concentration and amount with depth in the soil layers (Lousier and Parkinson, see footnote 1). Fe concentrations and C:Fe ratios in the decomposing litter reached L layer levels only after 60 months. C:Fe generally decreases throughout 60 months of decomposition in both litter types. No critical values are apparent because Fe accumulates throughout the study period. Soil Mn:Fe ratios were similar in the L, F, and H layers but decreased sharply in the Ah. After a sharp drop after 5–8 months of decomposition, the Mn:Fe ratios in the leaf litter were similar for the remainder of the study period, indicating a more rapid initial accumulation of Fe than Mn but similar rates of accumulation throughout the bulk of the study period. Gosz *et al.* (1973) stated that the leaves of species more susceptible to decomposition accumulated more Fe than those less susceptible. In the present study, the balsam leaves accumulated more Fe than did aspen leaves but had a lower rate of dry weight loss. Accumulation of Fe in aspen and balsam leaves was positively and significantly (p = 0.05) correlated with dry weight loss (r = 0.9748 for aspen, 0.9402 for balsam). Fe has been found to accumulate slightly in fungal sporocarps and slime molds, very heavily in rhizomorphs (Stark 1972), and in bacteria (Patrick and Loutit 1972). Cromack *et al.* (1975) found no accumulation of Fe in fungal vegetative or reproductive structures, and Hinneri (1975) reported the Fe content of macrofungi to be similar to that of higher plants.

Zinc

This element showed no differences between species except that the weight of Zn had dropped below the initial value *by* 48 months in aspen and *after* 48 months in balsam litter. While Zn concentrations doubled after 48 months, the amounts of Zn were constant for 48 months in both types of litter. Gosz *et al.* (1973) found about a 1.5- to 2-fold increase in weight of Zn in decomposing leaf litter of two of three species of tree while the third showed a net release of Zn from the time of deposition of the litter bags in the field. The third tree, yellow birch, was a Zn accumulator and its litter had amounts of Zn in excess of the Zn demand in the litter and soil layers. On the other hand, Töth *et al.* (1975) found concentrations and amounts of Zn fluctuated greatly over 12 months and attributed this to the interactions of leaching, increased microbial activities, and exchange capacities. Data from Cragg *et al.* (1977) showed an increase in Zn concentrations in aspen leaves over the summer. The C:Zn ratios of freshly fallen litter were similar in aspen and balsam, indicating, in comparison with data from Gosz *et al.* (1973), that there may have been some Zn accumulation in green aspen and balsam leaves, but perhaps not enough to fulfill the heterotroph Zn demand. C:Zn ratios decreased until 48 months and then increased dramatically in aspen and balsam, paralleling the pattern of change from the L to F to H layers in the woodland soil (Table 3). Critical C:Zn values were not apparent but probably would be greater than 3000:1 for aspen litter and 4000:1 for balsam litter. The pattern of concentration change paralleled those in the soil layers (Lousier and Parkinson, see footnote 1). The process of Zn accumulation has been reported to occur in fungal hyphae, rhizomorphs and sporocarps, and slime molds (Stark 1972; Todd *et al.* 1973; Cromack *et al.* 1975), and bacteria (Patrick and Loutit 1972). Zn has been considered to play an important role in several fungal metabolic processes (Cochrane 1958) and has been reported as the most abundant biologically significant trace element in macrofungi (Hinneri 1975) and the most readily accumulated trace element by these fungi (Byrne *et al.* 1976).

Sodium

Na is not generally thought to be an essential element in plant nutrition (Cromack *et al.* 1975); the Na content of plants is very low, regardless of the amount of Na in the soil (Miller and Flemion 1973). The Na contents of aspen and balsam leaves were low, as were those for Mn and Cu, and thus were difficult to detect accurately. The results were probably influenced more by plant chemical variability than by temporal or spatial variation due to decomposition.

Attiwill (1968) and Töth *et al.* (1975) found that Na was readily leached from decomposing litter, in fact as readily or more readily leached than K. Tukey (1970) reported that Na was readily leached from living plant tissue. Cragg *et al.* (1977) showed that Na increased in concentration (~50%) from June to late August but then decreased by 72% from late August to leaf abscission. Tew (1970) also measured an increase of Na concentration in aspen leaves, but over the entire growing season. There was, however, an order of magnitude difference between Tew's (1970) measurement of Na concentration at leaf senescence and the measured concentration of Na in leaves at leaf fall in this study. This was probably due to site differences, translocation of Na within the trees (Attiwill 1968), and (or) heavy losses through leaching at the time of leaf abscission. Na concentration in the decomposing litter attained the L and F layer concentrations after 30 months of decomposition. Soil Na concentrations remained low in the L and F layers but increased 20-fold in the H layer and doubled from the H to Ah layers (Lousier and Parkinson, see footnote 1). Gosz *et al.* (1976) also found Na to increase in the H layer. At 60 months decomposition the litter concentrations of Na had begun to register this expected increase.

Although Na proved to be highly leachable in these decomposition studies, the pattern of loss was quite different than that for K. The accumulation of Na over the first winter, beginning at zero time for aspen litter and after 1 month of decomposition in balsam litter, could possibly be attributed to Na input from rain, snow, and dust and to some lag in the release from the litter of Na to be leached. Perhaps the fall–spring diurnal freeze–thaw cycles are necessary to initiate large leaching losses of Na from plant litter. The winter accumulation phenomenon seemed to be restricted to fresh litter because no accumulation was noted at 12–18 months of decomposition (second winter). After the accumulation (after 5 months of decomposition) there was an immediate drop in weights of Na: 70% of the accumulated levels after 8 months and 85% after 18 months in aspen litter; 40% of the accumulated levels after 8 months and 70% after 18 months in balsam litter. Compared with the initial Na weights, the losses were 60 and 80% after 8 and 18 months respectively for aspen, and 0 and 40% respectively for balsam. The processes of net accumulation began again after 18 months, but more dramatically in aspen than in balsam. This process may have been effected by greater numbers of organisms, particularly saprophages (Reichle 1971; Carter 1975) and microorganisms, and (or) Na contained in precipitation, stemflow, and throughfall. Stark (1972) and Cromack *et al.* (1975) provided evidence identifying accumulation of Na by fungal rhizomorphs and sporocarps, even though Na is a nonessential element for fungi. Reichle (1971) reported Na concentrations in saprophages 17 times that in leaves, and Na is probably made more readily available to these invertebrates through accumulation first in the fungi.

C:Na ratios fluctuated considerably and after 60 months of decomposition were between the values of the F and H layer ratios. The minimum concentrations of Na indicated that critical C:Na values ranged from 33 400 : 1 for aspen to 21 600 : 1 for balsam litter.

Copper

Gosz *et al.* (1973) reported a general increase in Cu concentrations throughout the first 12 months of decomposition. Cu has been found to be firmly chelated by soil organic matter and accumulated in

TABLE 4. The effects of site aspect on elemental change (all figures in milligrams per gram) and C:N for aspen leaf litter

Aspect	Time, months	C	H	N	C:N	Ca	Mg	Cu	Fe	K	Mn	Na	Zn	P
North	0	492.9	61.0	10.5	46.9	22	2.6	0.006	0.07	7.4	0.05	0.04	0.22	2.2
	12	482.9	58.0	12.5*a*	38.6*ab*	35*a*	2.9	0.008	0.73*ab*	2.0*a*	0.11*a*	0.14*a*	0.31*a*	1.1*a*
	24	486.8	58.7	12.5	38.9	33	2.7	0.007	0.68	1.9	0.11	0.12	0.29	1.1
	36	474.4*b*	56.6	14.8*b*	32.1*ab*	35	2.2	0.009	0.61*b*	1.6	0.13*ab*	0.10*ab*	0.27*b*	1.1
South	0	492.9	61.0	10.5	46.9	22	2.6	0.006	0.07	7.4	0.05	0.04	0.22	2.2
	12	491.8	59.2	14.3*a*	34.4*ab*	35*a*	2.2	0.010	0.63*ab*	1.7*a*	0.11*a*	0.13*a*	0.33*a*	1.0*a*
	24	491.4	58.5	13.9	35.4	35	2.3	0.010	0.59	1.7	0.10	0.14	0.37	1.0
	36	441.9*ab*	53.6*a*	18.0*ab*	24.6*ab*	36	2.1	0.011	0.81*ab*	1.7	0.20*ab*	0.19*ab*	0.40*b*	1.2

NOTE: *a*, significant change with time within aspect ($p = 0.05$); *b*, significant difference at a given time between aspects ($p = 0.05$).

the surface soil layers in forests (Stone 1968). In the soil layers in the aspen soil, Cu concentrations increased only slightly from L to F to H, but tripled from H to Ah, thus being accumulated only in the layer (Ah) with the lowest amount (10%) of organic matter.

Cu was the least abundant element studied in the aspen and balsam litter. The Cu concentrations in aspen and balsam were generally constant for the first 36–48 months and then increased to levels approaching those in the Ah. Accumulation of Cu occurred only in balsam litter; perhaps the balsam leaves, being more robust than aspen leaves, retained structural integrity longer and were able to chelate Cu more readily. Leaching appears to have been inconsequential as an agent of Cu release, although Cu concentrations in green aspen leaves decreased during the summer by more than 50% (Cragg *et al.* 1977). The primary source of Cu might have been the parent material. Cu has been reported to be accumulated by sporocarps (Stark 1972; Cromack *et al.* 1975), rhizomorphs and slime molds (Stark 1972), macrofungi (Hinneri 1975; Byrne *et al.* 1976), bacteria (Patrick and Loutit 1972), and invertebrates (Wieser *et al.* 1976).

C:Cu levels in decomposing aspen leaves generally followed the decreasing pattern of C:Cu in the soil layers but there were some wide deviations from the pattern. L layer C:Cu levels were reached in decomposing aspen litter after 8 months. Balsam litter C:Cu ratios adhered more closely to the decreasing pattern and the C:Cu ratio after 60 months had reached H layer levels. Critical C:Cu ratios were not readily apparent but probably reached 100 000 : 1 and 75 000 : 1 for aspen and balsam litter respectively.

Effect of Site Aspect

Table 4 briefly shows a comparison of some elemental concentrations in aspen leaf litter that had all been collected during leaf fall at the same site (i.e., the main aspen site (see Lousier and Parkinson 1976)) but which had been placed out in litter bags for 12, 24, and 36 months in sites of different aspect (i.e., the auxiliary aspen plots (see Lousier and Parkinson 1976)). After 36 months, the concentration of C was lower in litter placed on south-facing sites and the concentration of N was higher in the same litter, giving a significantly lower C:N ratio. The other elements affected (Fe, Mn, Na, Zn) all had significantly greater concentrations after 36 months of decomposition in the aspen litter placed on southern slopes than that placed on the northern slopes.

The lower C:N ratios in litter on the south-facing slopes indicated a greater dry weight loss than on northern slopes; these results were verified in Lousier and Parkinson (1976). The four other elements affected were all elements that were accumulated to a great degree. The concentrations of these elements in the north-facing sites may have been affected by several factors: closer proximity to the dusty road, prevailing winds, and slower nutrient release (lower dry weight loss, lower soil temperatures, possibly lower levels of microbial activity). Leaching effects appeared not to have been influenced although soil and litter moisture levels were usually significantly ($p = 0.05$) higher on the north-facing slopes (unpublished data). Immobilization appears to be controlled mainly by temperature as long as moisture conditions are adequate (Witkamp 1969*a*).

Elemental Change in Aerial Bags

Table 5 gives the chemical analyses of aspen leaf litter in aerial bags after 3 months (midwinter) and 10 months in the field. Moisture contents and fungal growth in the aerial bags were very substantially and significantly lower than those in the litter bags on the forest floor (S. Visser, personal communication). From visual observations, it appeared as if little physical change had occurred after 10 months, i.e., little apparent decomposition. However, no estimate of dry weight loss was possible for the aerial bags.

N, Ca, Mn, and Zn concentrations increased, P, K, and Mg concentrations decreased, Na and Fe concentrations increased at 3 months and then decreased, and Cu concentration decreased at 3 months and then returned to the initial level. In the

TABLE 5. Changes in concentrations of elements (milligrams per gram) and C:N in decomposing aspen litter in aerial bags

Time, months	C	H	N	C:N	Ca	Mg	Cu	Fe	K	Mn	Na	Zn	P
0	497.2	62.0	9.8	50.7	22.5	2.7	0.030	0.18	9.3	0.04	0.18	0.78	0.9
3	497.0	61.4	10.7	46.4	24.6	2.6	0.020	0.36	6.1	0.05	0.22	0.45	0.7
10	485.3	59.2	15.2	31.9	32.2	2.0	0.032	0.30	1.8	0.08	0.12	0.74	0.4

soil surface litter bags, however, Mg concentrations were generally constant, Fe concentrations increased continually, and Cu concentrations were constant for 48 months before increasing.

Anderson (1973*a*) found that most of the dry weight loss from litter in aerial bags was accounted for by leaching and that the moisture content of the aerial bags was usually less than 10%, allowing only minimal levels of microbial activity. The dry weight loss recorded by Anderson (1973*a*) was, however, substantial. The annual precipitation totals for the Kananaskis area and the Blean Woods National Nature Reserve were similar, and one could perhaps assume that dry weight losses in the aerial bags in the Kananaskis region would approach the initial weight of the readily leached component, W_l (Lousier and Parkinson 1976, Fig. 4), of aspen leaves, i.e., about 20% after 10 months' decomposition.

After 10 months, the concentration of N was up 95% over the initial value, Ca 43%, Fe 65%, Mn 105%, and Zn 64%. Thus it was obvious that these five elements accumulated in weight in the aerial litter bags over the course of 10 months; the sources of this accumulation have been discussed earlier. Mg concentrations declined 23%, K 80%, Na 36%, and P 56% after 10 months, the decreases being attributable primarily to leaching. Cu appeared to be leached significantly in the first 3 months but then started to accumulate.

Aerial bags of *Epilobium angustifolium* L. leaves produced results similar to those in this study (Krauter 1976). After 52 weeks, 90% of the K and P and 70% of the Mg had been leached, while Ca had accumulated to levels about 25% above the initial weight. The concentration of N decreased for 26 weeks but by 52 weeks had increased to levels above the original; the weight of N, however, remained relatively constant. Because there was a 40% dry weight loss over 52 weeks, the C:N ratio dropped from 64:1 initially to 29:1.

Anderson (1973*a*) stressed that leaching processes may be accentuated in aerial bags as a result of more frequent wetting and drying of the litter and by higher temperatures. This would appear to be a function primarily of the wettability of the dry leaves. Visual observations showed that the cuticle on the aspen leaves in aerial bags was mainly still intact after 10 months (S. Visser, personal communication), suggesting a lower wettability of the aspen leaves and less significant structural change due to wetting and drying than Anderson (1973*a*) proposed. Thus, only the periods of heaviest precipitation (long periods of continuous but light rainfall or shorter periods of heavy rainfall), as Witkamp and Olson (1963) indicated, could be significant (in terms of dry weight loss and leaching) to the 'slow-to-wet,' bagged aspen leaves.

Components of Elemental Change

The results of the elemental change over time studies in decomposing leaf litter can be integrated into the large-scale considerations of the aspen woodland site as a whole, starting with the figures for elemental input in leaf fall given in Lousier and Parkinson (1976). Such integration can provide some information on the net transfer of elements in decomposing leaf litter, i.e., when there is a net loss of element, through either leaching or decomposition or both, and when there is a net gain of element. This is shown in Fig. 2 for all the elements studied in aspen leaves only. Inputs from balsam leaves were much lower but the patterns for the two species were similar.

The calculations were made according to Gosz *et al.* (1973) and involved the same assumptions. Basically, the total element loss curve represents net leaching loss + net decomposition loss − net accumulation. The balance between these three elemental flow parameters is continually changing (Witkamp 1969*a*, 1969*b*), influenced by microbial community structure (Jansson 1958), activity and nutrient demand of the soil and litter organisms, environmental conditions regulating organism activity, plant species differences in tissue palatability and nutrient content, and differences in nutrient mobility (Gosz *et al.* 1973). The amount of element measured at any given time during decomposition is a manifestation of all these interactions.

Comparing the weights of elements at 60 months with those at 0 months of decomposition showed that the weight of K had decreased 88%, P 84%, Zn 70%, Mg 60%, Ca 36%, and N 31%, and that the weight of Na had increased 16%, Mn 35%, Cu 80%,

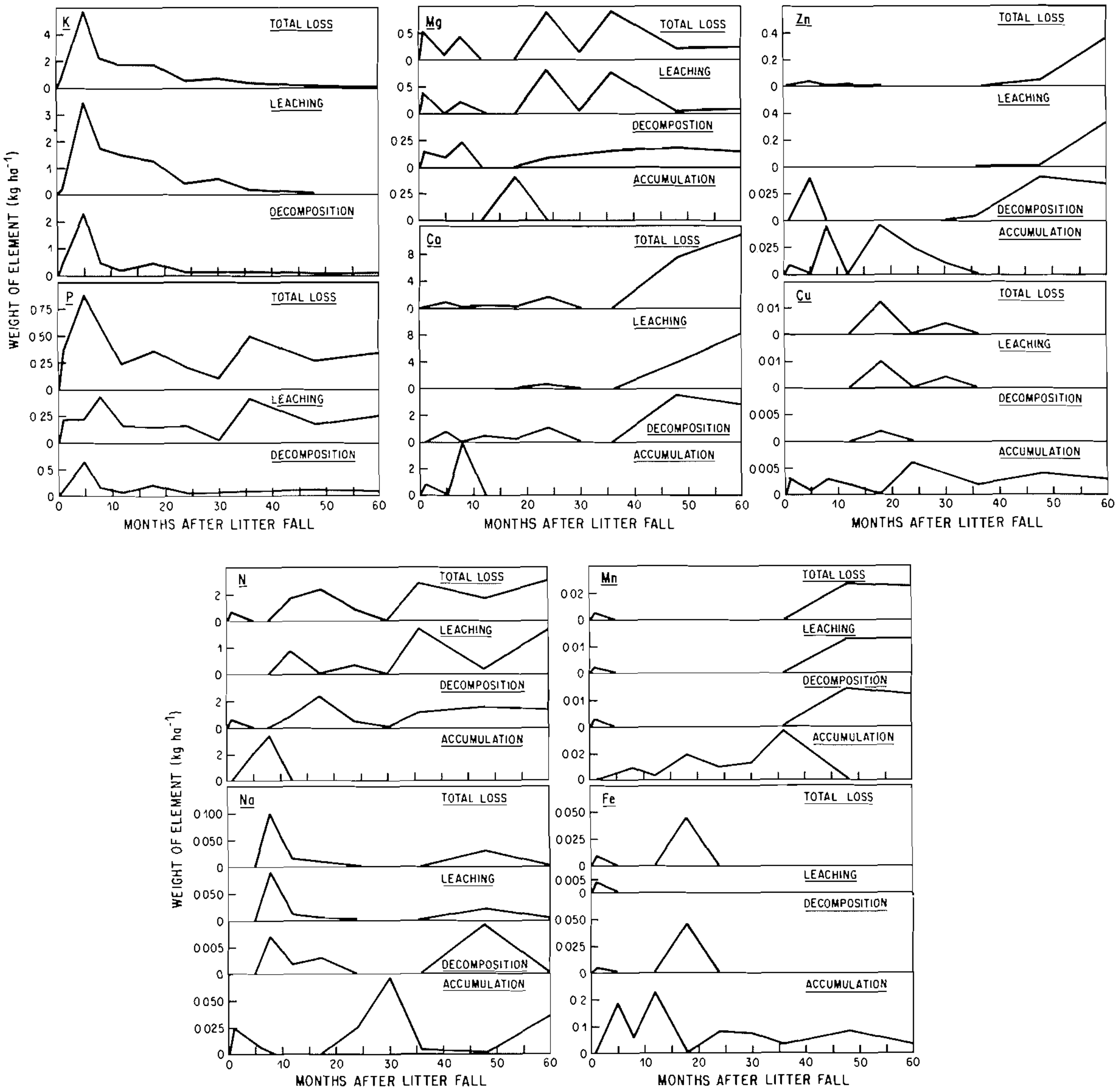

FIG. 2. The net transfer of chemical elements during the decomposition, over the first 60 months, of the annual increment of aspen leaf litter.

and Fe 516%. Leaching processes predominated in the autumn and spring with net leaching losses being recorded only at these times. While spring leaching may have accounted for greater leaching losses for some elements (particularly during the first spring), more elements were affected by leaching in the autumn months. Net decomposition losses occurred with equal frequency during the autumn and spring, slightly less in the winter months, and much less often in summer. The spring and summer months were the periods of most frequent net elemental accumulation, while the autumn and winter months were slightly less amenable for net accumulation processes. While the processes of leaching, decomposition, and accumulation may not appear to be always balanced in decomposing leaf litter, they are so in terms of the overall functioning of the soil organic layer in elemental conservation and cycling. Large leaching losses in the initial stages of litter decomposition do not mean losses to the ecosystem; the elements leached from surface litter are for the most part being accumulated biologically and (or) physicochemically in the lower organic layers, e.g., F and H.

Elemental Loss Models

Minderman (1968) suggested that the losses of the separate chemical constituents of decomposing litter may conform to a negative exponential function while total dry weight losses do not. The dry weight losses during the 1st year after leaf fall are large and cannot be fitted into the prediction of organic matter accumulation using a negative exponential function.

Results in Lousier and Parkinson (1976) indicated that the dry weight loss data from the decaying aspen and balsam leaf litter could be readily analyzed with the 'improved' negative exponential decomposition model of Bunnell and Tait (1974). It was also suggested that such a model may be most applicable to ecosystems with a low annual rate of litter decomposition, an absence or low incidence of litter comminution, and an easily determined leachable component. Krauter (1976) found that the dry weight loss data for *Epilobium angustifolium* leaves and stems in the same site were best described by a linear function ($r > 0.95, p < 0.001$). It is interesting, then, to compare the behaviour of the separate chemical elements and their rate of release with total dry weight loss, i.e., do elements follow a two-component loss pattern, a linear pattern, or no apparent pattern in decomposing leaf litter.

P, K, and Mg were shown to have some degree of correlation with dry weight loss in aspen and balsam litter, and the graphs in Fig. 1 suggested the possibility of a two-component loss pattern for these elements. Plotting the percentage of initial weight remaining on a logarithmic scale and regression analyses produced the following results: losses of K and P followed the two-component exponential loss pattern described by Bunnell and Tait (1974), while Mg losses showed no evidence of a two-component pattern; in fact, Mg followed a linear loss pattern ($p < 0.005$). Regression analyses of the behaviour of N, Ca, Mn, and Fe over time indicated that, for all these elements, accumulation patterns as well as loss patterns were linear ($p < 0.05$).

Further regression analyses of Krauter's (1976) chemical element loss data produced similar results: K and P loss patterns were linear ($p < 0.95$) or two-component, Mg loss was linear ($p < 0.0005$), and Ca accumulation was linear ($p = 0.05$). The two-component patterns were evident primarily in some of the aerial bags, where biological activity would have been considerably less and most losses could have been caused by leaching.

Modelling elemental loss data (such as those gathered, for example, in this study, Krauter (1976), Tóth *et al.* (1975), and Gosz *et al.* (1973)) has as its major limitation the situation in which the data were time series of the standing crops of elements in litter decompositing within litter and soil layers. None of the data represented an actual portion of the initial weight of element; rather, they measured the net manifestation of several processes: losses caused by leaching and decomposition, and accumulations caused by physicochemical mechanisms and biological activity. To overcome this limitation one must monitor all elemental inputs and outputs to and from the soil–litter subsystem and all leaching, decomposition, translocation, and accumulation rates within the subsystem; it is logistically a very difficult task.

Acknowledgment

We gratefully acknowledge financial support from NRCC operating grant No. A2257 over the duration of this project.

ALEXANDER, M. 1967. Introduction to soil microbiology. John Wiley & Sons, Inc., New York.

ALWAY, F. J., W. J. METHLEY, and O. R. YOUNGE. 1933. Distribution of volatile matter, lime and nitrogen among litter, duff, and leafmold under different forest types. Soil Sci. **36**: 399–407.

ANDERSON, J. M. 1973*a*. The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. I. Breakdown, leaching and decomposition. Oecologia (Berlin), **12**: 251–274.

——— 1973*b*. The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in the carbon, hydrogen, nitrogen and polyphenol content. Oecologia (Berlin), **12**: 275–288.

ATTIWILL, P. M. 1966. The chemical composition of rainwater in relation to the cycling of nutrients in mature *Eucalyptus* forest. Plant Soil, **24**: 390–406.

——— 1968. The loss of elements from decomposing litter. Ecology, **49**: 142–145.

AUSMUS, B. S., and M. WITKAMP. 1974. Litter and soil microbial dynamics in a deciduous forest stand. EDFB-IBP-73-10, Oak Ridge Natl. Lab., Oak Ridge.

BARSDATE, R. J., R. T. PRENTKI, and T. FENCHEL. 1974. Phosphorus cycle of model ecosystems: significance for decomposer food chains and effect of bacterial grazers. Oikos, **25**: 239–251.

BOCOCK, K. L. 1963. Changes in the amount of nitrogen in decomposing leaf litter of sessile oak (*Quercus petraea*). J. Ecol. **51**: 555–566.

——— 1964. Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J. Ecol. **52**: 273–281.

BOYD, C. E. 1971. The dynamics of dry matter and chemical substances in a *Juncus effusus* population. Am. Midl. Nat. **86**: 29–45.

BUNNELL, F. L., and D. E. N. TAIT. 1974. Mathematical simulation models of decomposition processes. *In* Soil organisms and decomposition in tundra. *Edited by* A. J. Holding, O. W. Heal, S. F. Maclean, Jr., and P. W. Flanagan. Tundra Biome Steering Committee, Stockholm.

BURGES, A. 1956. The release of cations during the decomposition of forest litter. 6th Int. Congr. Soil Sci., Paris. Vol. B. pp. 741–745.

BYRNE, A. R., V. RAVNICK, and L. KOSTA. 1976. Trace element concentrations in higher fungi. Sci. Total Environ. **6**: 65–78.

CARLISLE, A., A. H. F. BROWN, and E. J. WHITE. 1966. Litter fall, leaf production, and the effects of defoliation by *Tortrix viridana* in a sessile oak (*Quercus petraea*) woodland. J. Ecol. **54**: 65–85.

——— 1967. The nutrient content of tree stem flow and ground flora litter and leachates in a sessile oak (*Quercus petraea*) woodland. J. Ecol. **55**: 615–627.

CARTER, A. 1975. Aspects of the population biology of *Agonum retractum* Leconte (Coleoptera: Carabidae) and its role and that of some other soil arthropods in the cycling of chemical elements in an aspen woodland ecosystem. Ph.D. Thesis, University of Calgary, Calgary, Alberta.

COCHRANE, V. W. 1958. Physiology of fungi. John Wiley & Sons, Inc., New York.

COLE, D. W., S. P. GESSEL, and S. F. DICE. 1967. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second growth Douglas-fir ecosystem. *In* Symposium on primary productivity and mineral cycling in natural ecosystems. *Edited by* H. E. Young. University of Maine, Orono.

CRAGG, J. B., A. CARTER, C. LEISCHNER, E. B. PETERSON, and G. N. SYKES. 1977. Litter fall and chemical cycling in an aspen (*Populus tremuloides* Michx.) woodland ecosystem in the Canadian Rockies. Pedobiologia, **17**: 428–443.

CROMACK, K., JR., R. L. TODD, and C. D. MONK. 1975. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. Soil Biol. Biochem. **7**: 265–268.

CURLIN, J. W. 1970. Nutrient cycling as a factor in site productivity and forest fertilization. *In* Tree growth and forest soils. *Edited by* C. T. Youngberg and C. B. Davey. Oregon State University Press, Corvallis.

DE KOCK, P. C. 1958. The nutrient balance in plant leaves. Agric. Prog. **33**: 88–95.

DENNIS, J. G. 1970. Aboveground accretion of vegetative and reproductive structures in an aspen understory vegetation in southwestern Alberta. Bull. Ecol. Soc. Am. **51**: 31.

DORMAAR, J. F. 1971. Prolonged leaching of orthic black Ah material with water and aqueous extracts of *Populus tremuloides* and *P. balsamifera* leaves. J. Soil Sci. **22**: 350–358.

DUVIGNEAUD, P., and S. DENAEYER-DE SMET. 1967. Biomass, productivity and mineral cycling in deciduous mixed forests in Belgium. *In* Symposium in primary production and mineral cycling in natural ecosystems. *Edited by* H. E. Young. University of Maine, Orono.

——— 1970. Biological cycling of minerals in temperate deciduous forests. *In* Analysis of temperate forest ecosystems. *Edited by* D. E. Reichle. Chapman and Hall, London.

GILBERT, O. J., and K. L. BOCOCK. 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. II. Changes in the nitrogen content of oak and ash leaf litter. J. Soil Sci. **11**: 10–19.

GOSZ, J. R., G. E. LIKENS, and F. H. BORMANN. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecol. Monogr. **43**: 173–191.

——— 1976. Organic matter and nutrient dynamics of the forest and forest floor in the Hubbard Brook Forest. Oecologia (Berlin), **22**: 305–320.

HARLEY, J. L. 1971. Fungi in ecosystems. J. Ecol. **59**: 652–668.

HINNERI, S. 1975. Mineral elements of macrofungi in oak-rich forests on Lenholm Island, inner archipelago of SW Finland. Ann. Bot. Fenn. **12**: 135–140.

HODKINSON, I. D. 1975. Dry weight loss and chemical changes in vascular plant litter of terrestrial origin, occurring in a beaver pond ecosystem. J. Ecol. **63**: 131–142.

JANSSON, S. L. 1958. Tracer studies on nitrogen transformations in soil with special attention to mineralization–immobilization relationships. K. LantbrHögsk. Annlr. **24**: 101–361.

JORGENSEN, J. R., and C. G. WELLS. 1973. The relationship of respiration in organic and mineral soil layers to soil chemical properties. Plant Soil, **39**: 373–387.

KARKANIS, P. G. 1972. Soils of the Kanasaskis Valley. Research Rep. 1, Environmental Sciences Centre (Kananaskis), University of Calgary, Calgary, Alta.

KING, H. G. C., and G. W. HEATH. 1967. The chemical analysis of small samples of leaf material and the relationship between the disappearance and composition of leaves. Pedobiologia, **7**: 192–197.

KIRBY, C. L. 1973. The Kanasaskis Forest Experiment Station, Alberta (history, physical features and forest inventory). Inf. Rep. NOR-X-51, N.F.R.C., C.F.S., Environ. Can., Edmonton, Alberta.

KORNEV, V. P. 1959. Accumulation of phosphorus and potassium within leaves of trees and shrubs and their leaching from litter during the autumn–winter period. Sov. Soil Sci. 1959: 469–476.

KRAUTER, K. J. 1976. Decomposition of *Epilobium angustifolium* L. in a cool temperate deciduous woodland. M.Sc. Thesis, University of Calgary, Calgary, Alta.

KUCERA, C. L. 1959. Weathering characteristics of deciduous leaf litter. Ecology, **40**: 485–487.

LEMÉE, G., and N. BICHAUT. 1973. Recherches sur les écosystèmes des reserves biologiques de la forêt de Fontainebleau. II. Décomposition de la litière de feuilles des arbres et libération des bioéléments. Oecol. Plant. **8**: 153–174.

LOUSIER, J. D. 1974. Effects of experimental soil moisture fluctuations on turnover rates of Testacea. Soil Biol. Biochem. **6**: 19–26.

LOUSIER, J. D., and D. PARKINSON. 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. **54**: 419–436.

LUTZ, H. J., and R. F. CHANDLER. 1946. Forest soils. John Wiley & Sons, Inc., New York.

MARCHENKO, A. N., and Y. M. KARLOV. 1963. Mineral exchange in spruce forests of the northern taiga and forest tundra of the Arkhangel 'Province.' Sov. Soil Sci. 1963: 722–734.

MCLEAN, E. O. 1975. Calcium levels and availabilities in soils. Commun. Soil Sci. Plant Anal. **6**: 219–232,

MILLER, E. V. 1957. The chemistry of plants. Reinhold Publishing Co., New York.

MILLER, L. P., and F. FLEMION. 1973. The role of minerals in phytochemistry. *In* Phytochemistry, inorganic elements and special groups of chemicals. Vol. III. *Edited by* L. P. Miller. Van Nostrand Reinhold Co., New York.

MINDERMAN, G. 1968. Addition, decomposition, and accumulation of organic matter in forests. J. Ecol. **56**: 355–362.

MITCHELL, M. J. 1974. Ecology of oribatid mites (Acari: Cryptostigmata) in an aspen woodland soil. Ph.D. Thesis, University of Calgary, Calgary, Alta.

OLSEN C. 1932. Studies of nitrogen fixation. 1. Nitrogen fixation in dead leaves of forest beds. C.R. Trav. Lab. Carlsberg, **19**: 1–36.

——— 1948. Adsorptively bound potassium in beech leaf cells. Physiol. Plant. **1**: 136–141.

OLSON, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, **44**: 322–331.

OVINGTON, J. D. 1968. Some factors affecting nutrient distribution within ecosystems. UNESCO, Nat. Res. Res. **5**: 95–105.

Patrick, F. M., and M. W. Loutit. 1972. Concentration of metals by a water bacterium of the genus *Sphaerotilus*. Proc. Univ. Otago Med. Sch. **50**: 30–31.

Rapp, M. 1971. Cycle de la matière organique et des éléments minéraux dans quelques écosystèmes méditerranéens. Progr. Biol. Int., Ecol. du Sol, C.N.R.S. Paris. pp. 23–184.

Reichle, D. E. 1971. Energy and nutrient metabolism of soil and litter invertebrates. *In* Productivity of forest ecosystems. *Edited by* P. Duvigneaud. UNESCO, Paris.

Reiners, W. A., and N. A. Reiners. 1970. Energy and nutrient dynamics of forest floors in three Minnesota forests. J. Ecol. **58**: 497–519.

Remacle, J. 1970. La microflore des litières. Bull. Soc. R. Bot. Belg. **103**: 83–96.

——— 1971. Succession in the oak litter microflora in forest at Mesnil-Eglise (Ferage), Belgium. Oikos, **22**: 411–413.

Remezov, N. P. 1959. Method of studying the biological cycle of elements in an oak forest. Sov. Soil Sci. 1959: 59–67.

——— 1961. Decomposition of forest litter and the cycle of elements in an oak forest. Sov. Soil Sci. 1961: 703–711.

Rochow, J. J. 1975. Mineral nutrient pool and cycling in a Missouri forest. J. Ecol. **63**: 985–994.

Ryden, J. C., J. K. Syers, and R. F. Harris. 1973. Phosphorus in runoff and streams. Adv. Agron. **25**: 1–45.

Stark, N. 1972. Nutrient cycling pathways and litter fungi. BioScience, **22**: 355–360.

Stone, E. L. 1968. Microelement nutrition of forest trees: a review. *In* Forest fertilization, theory and practice. Tennessee Valley Authority Natl. Fertilizer Development Center, Muscle Shoals, Alabama.

Tew, R. K. 1970. Seasonal variation in the nutrient content of aspen foliage. J. Wildlife Manage. **34**: 475–478.

Thomas, W. A. 1969. Accumulation and cycling of calcium by dogwood trees. Ecol. Monogr. **39**: 101–120.

——— 1970. Weight and calcium losses from decomposing tree leaves on land and in water. J. Appl. Ecol. **7**: 237–241.

Tisdale, S. L., and W. L. Nelson. 1966. Soil fertility and fertilizers. Macmillan Co., New York.

Todd, R. L., K. Cromack, Jr., and J. C. Stormer, Jr. 1973. Chemical exploration of the microhabitat by electron probe microanalysis of decomposer organisms. Nature (London), **253**: 544–546.

Töth, J. A., L. B. Papp, and B. Lenkey. 1975. Litter decomposition in an oak forest ecosystem (*Quercetum petraeae cerris*) of northern Hungary studied in the framework of "Sikfökut Project." *In* Biodégradation et humification. *Edited by* G. Kilbertus, O. Reising, A. Mourey, and J. A. Cancela da Fonseca. Pierron Editeur, Sarreguemines.

Tukey, A. B., Jr. 1970. The leaching of substances from plants. Annu. Rev. Plant Physiol. **21**: 305–332.

Ulrich, B., R. Mayer, and M. Pavlov. 1971. Investigations on bioelement stores and bioelement cycling in beech and spruce stands including input–output analysis. *In* Systems analysis in northern coniferous forest—IBP Workshop. *Edited by* T. Rosswall, Kuatte, Masugn, Sweden. Bull. Ecol. Res. Comm. **14**: 87–113.

Uhrstrom, I. 1969. The time effect of auxin and calcium on growth and elastic modules in hypocotyls. Physiol. Plant. **22**: 271–287.

Van Cleve, K., and L. L. Noonan. 1975. Litter fall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. Can. J. For. Res. **5**: 626–639.

Wallace, A., and R. T. Mueller. 1962. Effects of magnesium concentration on *in vitro* CO_2 fixing reaction. Plant Physiol. **37**: 154–157.

Wieser, W., G. Busch, and L. Buchel. 1976. Isopods as indicators of copper content of soil and litter. Oecologia (Berlin), **23**: 107–114.

Wilde, S. A. 1958. Forest soils—their properties and relation to silvi-culture. Ronald Press Co., New York.

Will, G. M. 1967. Decomposition of *Pinus radiata* litter on the forest floor. 1. Changes in dry matter and nutrient content. N.Z. J. Sci. **10**: 1030–1044.

Witkamp, M. 1969*a*. Environmental effects on microbial turnover of some mineral elements. Part I—Abiotic factors. Soil Biol. Biochem. **1**: 167–176.

——— 1969*b*. Environmental effects on microbial turnover of some mineral elements. Part II—Biotic factors. Soil Biol. Biochem. **1**: 177–184.

Witkamp, M., and J. S. Olson. 1963. Breakdown of confined and nonconfined oak litter. Oikos, **14**: 138–147.

Wohler, J. R., D. B. Robertson, and H. R. Laube. 1975. Studies on the decomposition of *Potamogeton diversifolius*. Bull. Torrey Bot. Club, **102**: 76–78.

Wood, T. G. 1974. Field investigations on the decomposition of leaves of *Eucalyptus delegatensis* in relation to environmental factors. Pedobiologia, **14**: 343–371.